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Palaeontology: Which Came First, the Pterosaur or the Egg?

Pterosaur fossils are among the rarest and their eggs are even rarer. How then can we get an insight into the lifestyle of these flying reptiles? A wealth of new pterosaur fossils, including eggs, from China now provides exactly that.

David M. Martill

Pterosaurs are among the most awe inspiring of the archosaurian reptiles, vying with *Tyrannosaurus rex* and *Velociraptor* for a place at the top of the prehistoric popularity chart. The first pterosaurs described in the late 18th and early 19th centuries [1,2] were compared to the fiend of Dante's *Inferno* [3] despite their rather small size. Later discoveries, however, hinted at wingspans of more than 6.5 meters [4], and pterodactyls, more properly called pterosaurs, quickly became the dragons of popular folklore, and with star performances in Arthur Conan Doyle's *The Lost World* and Michael Crichton's *Jurassic Park*. Knowledge of the palaeoecology of pterosaurs has advanced at a painstakingly slow pace and their evolutionary relationships with other archosaurs, as well as within the Pterosauria, remain controversial [5]. Biomechanical studies of their flight had begun very early based on mathematical modelling of some extremely well preserved examples from the chalk of Kansas [6], but analysis of other aspects of their

lifestyle, such as feeding and reproductive strategies, remain in their infancy even after more than 200 years of study. Now, in a recent issue of *Current Biology*, Wang et al. [7] report an extraordinary discovery of multiple partially articulated skeletons of a new genus and species of pterosaur named *Hamipterus tianshanensis*, associated with three-dimensionally preserved eggs.

Hardly any cases have been reported of well-preserved pterosaurs occurring as more than a single skeleton. Sure, there are a few bone beds with concentrations of pterosaur bones, most notably the Cretaceous Cambridge Greensand of England, but these deposits are a chaotic mix of very worn and broken fragments of at least five genera and it's the Devil's own job to sort out which bone belongs to which genus [8]. An exciting aspect of the discovery reported by Wang et al. [7] is that several exceptionally well preserved pterosaurs pertaining to a single taxon are associated, appearing to represent mature sub-adult and adult individuals. And what's more, at least five

extremely well preserved eggs are mixed in with the bones.

Eggs First

Until ten years ago, the only evidence that pterosaurs laid eggs with mineralised shells — as opposed to soft-shelled eggs or giving birth to live young — came from phylogenetic analyses that showed pterosaurs as a sister taxon to Dinosauria forming the clade Ornithodira (but usually called Avemetatarsalia [9]). This clade comprising dinosaurs, birds and pterosaurs is in turn a sister clade to one that includes extant crocodiles. Thus, in the great tree of life, pterosaurs lie between crocodiles and birds, both of which lay eggs with a calcite shell. Parsimony thus suggests that pterosaurs too laid eggs with a calcite shell. Known as extant phylogenetic bracketing, the assumption is that birds and crocodiles inherited calcite shelled eggs from a shared common ancestor and pterosaurs should also have done so. However, it is possible that the pterosaur clade might at some time in their early evolution have lost the shelled egg, perhaps laying soft eggs, or perhaps not even laying eggs at all. The fossil record might just throw up a soft-shelled egg, but live birth would require the death and preservation of a gravid female, known for ichthyosaurs, but not for pterosaurs.

The first discovery of a fossil pterosaur egg came from the Early



Figure 1. Pterosaur males and females protected eggs?

A male example of the new pterosaur *Hamipterus tianshanensis* proudly displays its prominent headcrest (bottom) and a more moderate version thereof in a female (top). A unique fossil site in the Cretaceous Tugulu Group in China's Xinjiang province reveals a mass death assemblage of more than 40 individuals including males and females, some immatures and five 3D preserved, thin shelled eggs. This unique site changes our perceptions of pterosaur breeding habits. Reconstruction by Chuang Zhao.

Cretaceous Yixian Formation in China [10]. The nature of the eggshell was not described in detail, but in the same year a second pterosaur egg was described from the same formation with a soft and leathery shell, like that of some turtles and squamates [11]. However, a third pterosaur egg discovered in Early Cretaceous strata of Argentina appeared to show a thin calcitic layer, albeit only 30 microns thick [12]. There is no doubt that these eggs are from pterosaurs, as they all contain recognisable pterosaur embryos. But it seems one egg has a thin calcitic shell while another doesn't. This can be interpreted in two ways. Either, it could be a real signal, and that some pterosaurs laid thin shelled eggs while others laid soft, leathery eggs. The distinction could be taxonomic as the Argentinian egg is from a ctenochamatid pterosaur whereas the Chinese eggs were

attributed to ornithocheirids. This taxonomic distinction could be important, suggesting different egg structures for different taxonomic groups. Alternatively, the difference could simply reflect taphonomy and not a real biological difference. All of these discoveries had been flattened by overburden pressure, and subject to possible diagenetic change as a consequence. Such changes can include the dissolution of the original egg's shell, or the precipitation of mineral growths on to organic templates (often called 'beef'), which make interpretation of the original egg-shell structure difficult.

The eggs of *Hamipterus*, an ornithocheirid, now described by Wang *et al.* [7] are preserved in 3D and show localised squashing, rather than uniaxial compaction over the entire egg as in all the other

discoveries. The shell is preserved and shows numerous small cracks where it has been squashed. Thus, it seems as though pterosaur eggs were indeed mineralised, albeit thinly, and that they were really very delicate. A few years ago, a Chinese pterosaur (*Darwinopterus modularis*) from Jurassic strata was discovered associated with an egg-like object adjacent to the skeleton, almost as if it had been expelled after death [13]. Although lacking an embryo, this was the first example of an egg associated with a pterosaur and thus provided the first undisputed example of a female pterosaur.

Dimorphic Pterosaurs

Sexual dimorphism had been suspected for many years for pterosaurs, but difficult to prove. The often bizarre head crests of many pterosaurs had been taken to be evidence of sexual selection for ornaments in males [14]. Detailed statistical analyses of *Pteranodon ingens* seemed to show two morphs among larger forms, one with a narrow pelvis and the other with a wider, open pelvis [15]. It was assumed that the larger, open pelvic structure enabled egg laying, and thus represented the female of the species. The single female of *Darwinopterus* also has an open pelvis [14].

Hamipterus tianshanensis [7] clearly represents a new taxon. The skulls in the assemblage all possess a bony sagittal crest on the anterior rostrum, but it is highly variable in size, shape and robustness. (Figure 1). Some of the crests are mere low bony ridges, but others are high, directed forwards in a sweeping arch with fibrous dorsal margins. It remains to be determined beyond doubt which condition is male and which is female, or if the low condition is merely juvenile, but with more than 40 individuals in the assemblage a more thorough morphometric analysis will surely yield exciting results. The authors have opted for males possessing the high, robust crest — not an unreasonable assumption given what we know about ornamentation in male animals in general that merely awaits matching a pelvis to a skull to be tested. The most exciting feature about this assemblage is that males and females are preserved together along with the eggs. This strongly

hints at a prolonged courtship with males hanging around after fertilising the 'hens', perhaps to assist with rearing the young, perhaps feeding the hen during incubation; although the authors prefer that rather than being incubated bird-style the eggs were buried in the soft sediment, much like other reptiles do, as suggested by studies on predicted vapour conductance of pterosaur eggshells [16] and by assumptions about eggshell strength [17].

The phylogenetic analysis performed on *Hamipterus* allies it with such famous pterosaurs as the edentulous *Pteranodon* (the one with the big pointy head crest) from North America and *Ornithocheirus*, a toothy European form with a crest on the tip of its beak and made famous in the BBC TV blockbuster *Walking With Dinosaurs*. This group of pterosaurs, known as ornithocheiroids (although they are termed pteranodontians by Wang *et al.* [7]), were widespread during the Early Cretaceous and survived almost to the end of the period, which also marked the end of the dinosaurs. Most ornithocheiroids were very large with a wingspan in excess of 4 metres, and perhaps over 7 metres [18], but *Hamipterus* is comparatively small with a wingspan estimated to have been between 1.5 and 3.5 metres. An unusual aspect of *Hamipterus* as an ornithocheiroid is the nature of its rostral crest. Most ornithocheiroids possess a crest (located either on the upper and lower jaw tips, e.g. *Coloborhynchus*, on the posterior cranium, e.g. *Ludodactylus*, or both, e.g. *Caulicephalus*), and in all cases the margin of the crest is entire, sharply defined and the bone surface smooth (although it may contain channels for depressed veins and arteries). This contrasts strongly with the irregular margin and fibrous bone of *Hamipterus*' crest, and is of a type found in Dsungaripterids and some non-pterodactyloid pterosaurs, including *Darwinopterus*. Despite this anomaly, almost all other aspects of *Hamipterus*' skeleton do indicate ornithocheiroid affinities.

The authors have identified the remains of more than 40 individuals in the deposit so far, which is

unprecedented for a pterosaur site. Hundreds more probably remain to be found. Never before have so many remains attributed to a single taxon been found in such close association, and in the presence of eggs. This discovery represents a unique opportunity to investigate pterosaur growth, development, reproductive behaviour and ecology. Expect many more papers on this amazing deposit when the sedimentology and taphonomy have been studied in detail.

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Sex Determination: Ciliates' Self-Censorship

Differentiation involves the expression of certain latent cellular characteristics and the repression of others. A new study has revealed how *Paramecium* uses short RNAs to delete information from the somatic genome of one of its two sexes.

Gareth Bloomfield

Sex involves the most fundamental kind of differentiation in biology. Most interbreeding populations are divided into separate classes of organism that are mutually sexually

compatible: sexes or mating types. Crucially, gametes must be different enough for their correct partners to be distinguished. Although in many organisms sperm and egg cells are different in size and shape, unicellular species typically